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Clinal variation and subspeciation in the White-crowned Black Wheatear *Oenanthe leucopyga*

by Alan Tye

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The type specimen of the White-crowned Black Wheatear *Oenanthe leucopyga* (C. L. Brehm, 1855) was collected at Korosko, Egypt, a locality now submerged in Lake Nasser (22°40′N, 32°20′E). Hartert (1913) later described a race *O.l. aegra* (type from Algeria) on the basis of smaller size. Meinertzhagen (1930) claimed that no size difference existed between nominate and *aegra* and suppressed the latter, but at the same time he described a new subspecies, *O.l. ernesti,* from Sinai and Palestine (type from Sinai) distinguished by a longer bill and bluer, glossier plumage. Meinertzhagen's arrangement has been generally followed since, though most authors (e.g. Vaurie 1959, White 1962) have pointed out that *ernesti* is not clearly separated, but intergrades with nominate in Egypt. Vaurie (1959) also suggested that *ernesti* had larger, darker spots near the tips to the outer rectrices.

In the present paper I examine clinal variation in size, colouration and tail pattern in this species, and the implications of such variation for subspecific nomenclature. The results presented here refer to specimens at the British Museum (Natural History).

Distribution

For the purpose of analysing clinal variation I divided the species' range into 9 populations, some of which correspond with natural 'gaps' in the range (Fig. 1), where the habitat is unsuitable for breeding, or where the species seems to be either absent or present at very low densities. Such gaps occur in the western Egyptian desert (between populations 2 and 3), the Gulf of Suez (between 3 and 4), highland Eritrea (between 6 and 7), lowland western Sudan (between 6 and 8: cf. Lynes 1925) and lowland Sahara (between 8 and 9, 9 and 1/2). In addition, population 9 consists of several sub-populations on each of the central Saharan massifs, separated from one another by lower, flatter, sandier country, where the species does not breed.

Size

Clinal variation in size is shown in Figs. 2 and 3 and the Appendix. Trends are generally clearer for males, of which I was able to examine larger samples. In general, size increases from west to east across north Africa and into Arabia. Size decreases southwards through northeast Africa from Egypt to eastern Sudan, and decreases further from eastern Sudan westward through the Sahara (compare Figs. 2 and 3 with Fig. 1). The largest birds are found in Arabia and the smallest in northwest Africa and the central Sahara. This pattern applies to wing, tail and bill measurements. In contrast, the trends in tarsal length are a mirror image of these, with Arabian birds having some of the shortest tarsi. The sample from Eritrea/Djibouti (population 7) comprised only 5 males and 2 females, and few conclusions can be drawn from it.

Figure 1. The breeding range of the White-crowned Black Wheatear *Oenanthe leucopyga*. Populations: 1. Northwest Africa; 2. Libya & northwest Egyptian oases; 3. Egypt and north Sudan Nile Valley; 4. Sinai, Israel & Jordan; 5. Arabia; 6. Eastern Sudan, including Jebel Elba; 7. Eritrea (Danakil) & Djibouti; 8. Darfur, including east Chad; 9. Central Saharan massifs.

Plumage

Plumage differences are a matter of degree. In general, the black areas of the plumage of birds from populations 1, 2, 8 and 9 are dull, while in most individuals of populations 4 and 5 they have a pronounced glossy blue sheen. The other populations are intermediate, with some dull individuals, some very glossy and others in between. These differences apply when individuals in comparable stages of plumage wear are compared, though plumage colours are not greatly affected by wear.

Vaurie (1959) wrote that the "black spots on tips of outer rectrices" were "larger and deeper black, longer on outer web" in *ernesti*. In fact, the amount of brown in the tail is very variable in all populations. Variation occurs in 4 ways: 1) the number of rectrices having brown spots at the tips,

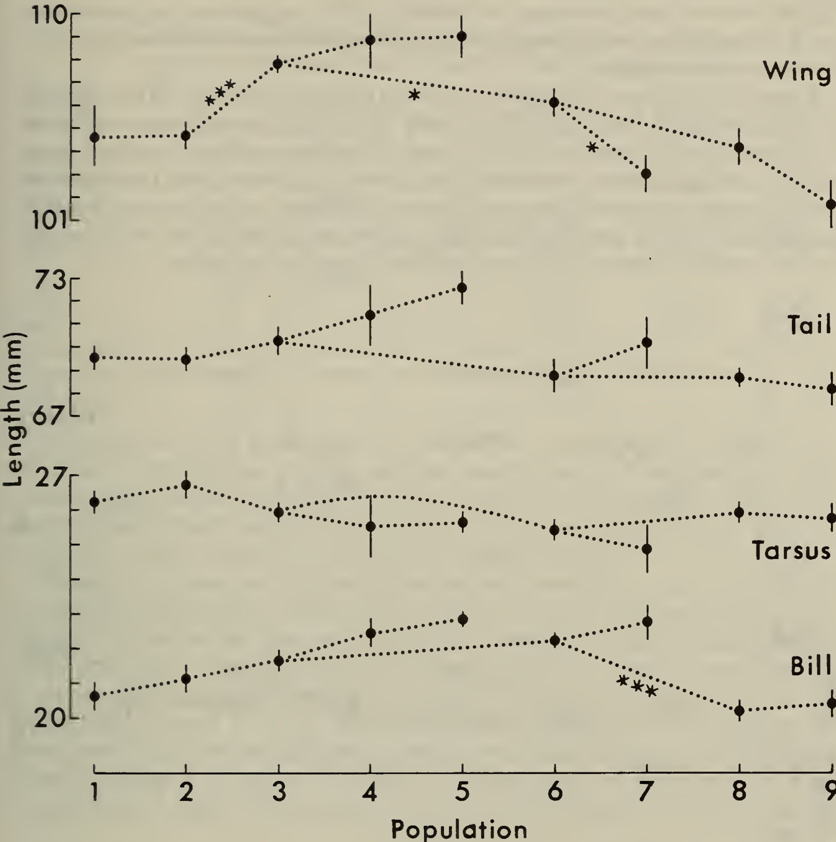

Figure 2. Clinal variation in size of male White-crowned Black Wheatears *Oenanthe leucopyga*. Numbers below the abscissa refer to the populations in Fig. 1. Dotted lines link geographically-adjacent populations; bars show mean±1SE. Statistically-significant differences in size between adjacent populations are shown by asterisks: *$P<0.05$, **$P<0.01$, ***$P<0.001$ (2-tailed t-tests). Full data for Figs. 2 & 3, plus ranges of variation and sample sizes, are given in the Appendix.

2) whether the brown is present on one or both webs, 3) whether the brown is smudgy or solid, 4) the size of the brown spots. I examined each of these possibilities, ignoring the central pair of tail feathers, which carries a consistently large area of brown.

The number of rectrices with brown spots near the tips can vary from 1 to 5 (on each side), ignoring the brown central pair. Where the 2 sides of a bird's tail differed, I took the larger figure. Nearly all populations showed a bimodal distribution of this attribute, peaking at 2 (with rectrices 2 and 6, numbering centrifugally, having brown spots) and 5 (all (2-6) having brown spots). Because of this, and the relatively small samples, I grouped the data into birds with 0-2 rectrices having spots and 3-5 having spots.

Table 1 shows that, contrary to Vaurie's (1959) suggestion, populations 4 and 5 (*ernesti*) have a higher proportion of individuals with fewer spots; i.e. they have whiter tails.

Rectrices with spots can have a mark on one or both webs. When scoring for this character, I scored a tail as 'both' if the mark spread onto both webs in at least one tail feather. Table 2 shows that this attribute is rather more variable, with different patterns in the 2 sexes, suggesting that there are few real differences between the populations. However, in both sexes, western populations 1, 2, 8 and 9 have a high proportion of individuals with brown on both webs, which is again contrary to Vaurie's suggestion.

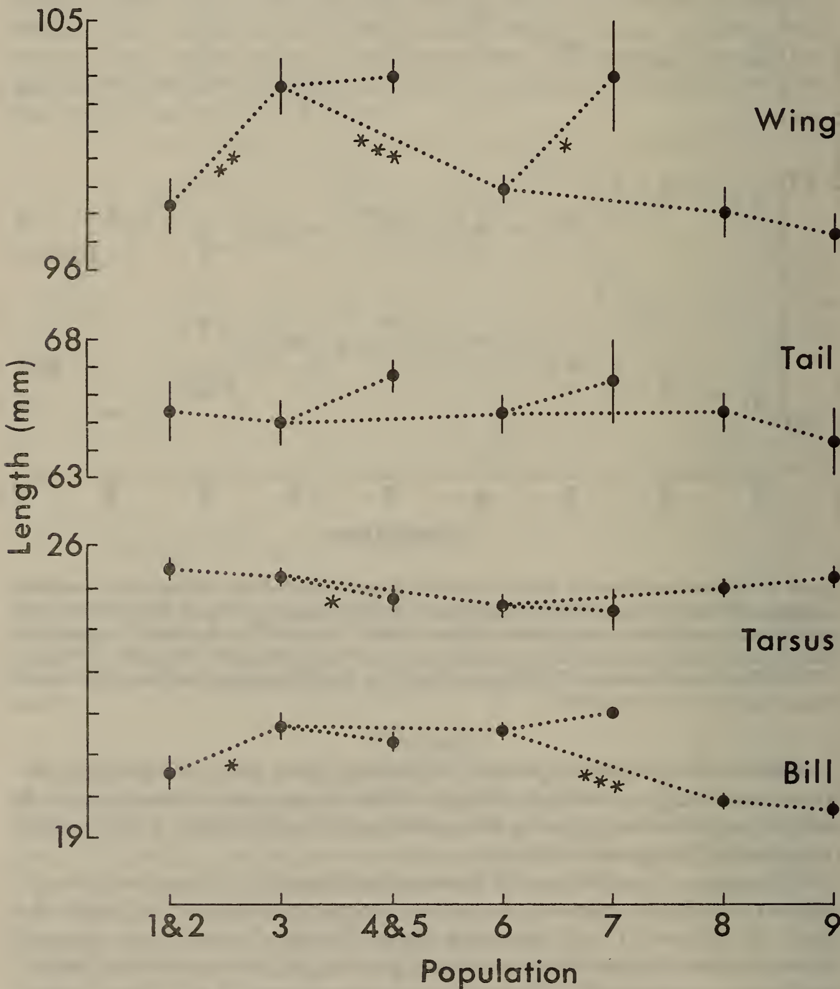

Figure 3. Clinal variation in size of female White-crowned Black Wheatears *Oenanthe leucopyga*. Symbols as in Fig. 2.

TABLE 1

Number of outer tail-feathers with brown spots in *Oenanthe leucopyga* populations (see text and Fig. 1). Figures in brackets are percentages

	Populations									western	central	eastern
	1	2	8	9	3	6	7	4	5	1, 2, 8, 9	3, 6, 7	4, 5
No. with spots	Males											
0–2:	7	3	1	0	7	3	0	2	6	11 (31)	10 (28)	8 (47)
3–5:	3	6	10	6	4	17	5	3	6	25 (69)	26 (72)	9 (53)
	Females											
0–2:	2	0	0	0	4	2	0	0	5	2 (9)	6 (21)	5 (50)
3–5:	6	1	10	3	7	13	2	1	4	20 (91)	22 (79)	5 (50)

X^2 tests for populations 4 & 5 (= *ernesti*) *vs* the rest: males $X_1^2=1.27$, N.S.; females $X_1^2=3.85$, $P<0.05$.

I scored tail spots as smudgy or solid brown subjectively, weighting the decision towards the pattern on the outermost pair of feathers. This character shows no coherent pattern, except that population 7 has consistently very dark tails (Table 2). This is also inconsistent with Vaurie's suggestion that *ernesti* has tail spots of a deeper shade.

Finally, I measured the length of brown parallel to the shaft on the outermost tail feather (taking the greater of the measurements on the 2 sides) as an index of spot size (Table 3). Probably owing to small sample sizes and great intra-population variability, there is again inconsistency between the patterns shown by the 2 sexes. However, it is clear that eastern populations 4 and 5 do not have consistently longer brown marks on the rectrices than other populations, contrary to Vaurie's suggestion. The only clear difference to appear in Table 3 is that birds of population 7 have exceptionally large spots, often covering half or more of the outer tail

TABLE 2

Brown spots (a) on one or both webs of tail-feathers, (b) smudgy or solid brown, in *Oenanthe leucopyga* populations (see text and Fig. 1). Figures in brackets are percentages

	Populations									western	central	eastern
	1	2	8	9	3	6	7	4	5	1, 2, 8, 9	3, 6, 7	4, 5
	Males											
a) on both webs	3	5	7	5	3	7	1	3	5	20 (56)	11 (31)	8 (47)
on one web	7	4	4	1	8	13	4	2	7	16 (44)	25 (69)	9 (53)
	Females											
on both webs	5	0	10	2	5	11	1	0	1	17 (77)	17 (59)	1 (10)
on one web	3	1	0	1	7	4	1	1	8	5 (23)	12 (41)	9 (90)
	Males											
b) smudgy	9	8	6	4	8	14	0	3	5	27 (75)	22 (63)	8 (47)
solid brown	1	1	5	2	3	6	5	2	7	9 (25)	13 (37)	9 (53)
	Females											
smudgy	6	1	3	1	9	9	0	1	7	11 (50)	18 (62)	8 (80)
solid brown	2	0	7	2	3	6	2	0	2	11 (50)	11 (38)	2 (20)

TABLE 3

Length of brown spot (mm) parallel to shaft on outermost tail-feather in *Oenanthe leucopyga* populations (see text and Fig. 1).

	Males				Females			
Population	Range	Median	Mean	n	Range	Median	Mean	n
1	0–10	5.5	5.0	10	0–12	7.5	6.0	8
2	0–11	4	4.6	9	6	6	6	1
8	6–17	13	12.5	11	9–22	14	14.9	10
9	5–12	7.5	7.8	6	5–16	11	10.7	3
3	0–14	5	5.4	10	2–21	6	10.8	12
6	4–17	7	7.9	20	0–19	14	12.5	15
7	21–51	27	33.8	5	31–33	32	32.0	2
4	3–18	10	11.0	5	6	6	6	1
5	4–19	12	11.1	12	0–15	6.5	7.2	9
1, 2, 8, 9	0–17	8	7.7±0.8	36	0–22	10	10.7±1.3	22
3, 6, 7	0–51	7	10.9±1.9	35	0–33	13	13.1±1.4	29
4, 5	3–19	10	11.1±1.2	17	0–15	6.5	7.1±1.4	10

feather. Indeed, there is no overlap between the range for the admittedly small samples from this population and the ranges of any of the others.

To summarise tail pattern: eastern (*ernesti*) populations do not have more brown on the tail than other populations, if anything, they have less. Population 7 stands out as having more tail feathers spotted, the spots darker brown and much larger than in any other population.

Subspeciation

The patterns discussed above reveal a central area, in Egypt, containing birds of intermediate characteristics, with smaller, duller birds to the south and west and larger, glossier birds to the northeast and east. This does not necessarily imply an Egyptian centre of origin for the species. These results confirm Hartert's (1913) findings of a size difference between western and Egyptian populations. In addition, they reveal an opposite trend in tarsal length from the trends in other measurements, which does not appear to have been noticed before.

The clines in size and plumage colouration do not show any obvious steps which could be used to divide the species sensibly into subspecies (except possibly in western Egypt), and the variation in tail pattern is not sufficiently clearly related to geographical distribution to allow subspecies to be based upon it, except possibly in the case of population 7. However, the natural gaps in the species range, which break the clines in size and plumage colour, permit the 9 populations to be grouped into 3 clusters.

First, populations 1, 2, 8 and 9 contain small, dull birds with long tarsi. Although it may appear from their distribution (Fig. 1) that 2 or more gene pools may exist here (e.g. 1/2 and 8/9), genetic exchange may occur if birds from the partially migratory northern populations winter in the central Sahara and remain there to breed. Such exchange must, however, be limited, as the central Saharan population 9 is smaller in size than the north African populations 1/2 (see Appendix), significantly so (t_{23}=2.660, P<0.02) in male wing-length. I was unfortunately unable to examine any specimens from the small breeding population in the Atar region of northern Mauritania, but measurements given by Dekeyser and Villiers (Dekeyser & Villiers 1950, Dekeyser 1954) place it firmly within this group and not, as suggested by these authors, with populations 3, 6 and 7 (8 males: wing 100.4±0.8, range 97–104; tarsus 24.8±0.7, range 22–28. 5 females: wing 98.0±1.9, range 92–102; tarsus 25.0±0.4, range 24–26 mm).

Although the geographical distance between populations 2 and 3 is small, there does seem to be a minor faunal barrier here, in the western Egyptian desert, where the ranges of several other taxa (including several wheatear *Oenanthe* spp or subspp) stop. The distance between populations 6 and 8 is greater, and its effectiveness as a barrier has been remarked upon by Lynes (1925). Hence populations 1, 2, 8 and 9 would seem to form a well-defined, rather isolated group of interlinked populations, having similar characteristics and being morphologically distinguishable from populations further east.

The second group of populations comprises 3, 6 and 7. Populations 3 and 6 are not well-separated from each other geographically, being linked in the upper Nile Valley and northeast Sudan. However population 7 is separated from 6 by highland Eritrea and appears to have diverged markedly in tail pattern and, to a certain extent, in morphology. It is included with populations 3 and 6 primarily for convenience. This group of populations is the most variable, even if population 7 is excluded from it, with individual birds having characteristics typical of each of the other 2 groups: this applies both to measurements and plumage characters.

The third and final group consists of populations 4 and 5. The main part of population 5 inhabits northern Saudi Arabia, with outliers in the east and south of the Arabian peninsula. There is no real geographical gap between populations 4 and 5, which seem morphologically indistinguishable from one another and form a homogeneous group.

Nomenclature

Brehm's type specimen was a member of population 3, an intermediate. The results presented above show that there are equally good grounds for distinguishing from the type Hartert's race *O.l. aegra* from northwest Africa, the central Sahara and Darfur (Lynes 1925), as there are for Meinertzhagen's race *O.l. ernesti* from Sinai, Palestine and Arabia. Since the type refers to an intermediate population and is, in fact, of an intermediate character (Vaurie 1959), the nominate subspecies could be taken to include either end of the range, or it could be restricted to intermediate populations alone. In view of this, Hartert's publication of the name *O.l. aegra* for a population which is recognizably different from the Egyptian (nominate) populations, would have the effect of restricting the nominate to either the intermediate population alone (i.e. 3, 6, 7), or to the entire population other than populations referrable to *aegra* (i.e. 3, 6, 7, 4, 5).

Meinertzhagen (1930), when stating his belief that there was no difference in size between western and Egyptian birds, in effect recognised

TABLE 4

Possible schemes for the subspecific nomenclature of *Oenanthe leucopyga*. Numbers refer to the populations in Fig. 1.

Scheme	*O.l. aegra*	*O.l. leucopyga*	*O.l. ernesti*
a)	1 2 8 9	3 6 7	4 5
b)	suppress	1 2 8 9 3 6 7 4 5	suppress
c) Hartert	1 2 8 9	3 6 7 4 5	suppress
d) Meinertzhagen	suppress	1 2 8 9 3 6 7	3 6 7 4 5

that there was. He referred to the western birds as nominate *leucopyga*, but on erecting his name *ernesti* for eastern birds he stated that Egyptian birds were *intermediate* between *ernesti* and western birds. That is, he recognized, implicitly, that Hartert was correct in differentiating western birds from Egyptian nominates. Hence, Meinertzhagen's action in suppressing a name for one end of the cline, while erecting a name for the other end seems perverse or, at least, illogical. His referral of all African populations to *O.l leucopyga* also obscures the range of variation which exists in Africa.

Of the possible schemes for subspecific nomenclature (Table 4), that of Meinertzhagen (scheme d) applying *O.l. leucopyga* to African populations and *O.l. ernesti* to Middle Eastern, with populations 3, 6 and 7 recognized as 'intermediates', seems inadmissible because *O.l. aegra* has priority over *O.l. ernesti* and if only one of these 2 races be recognised, it should be the first, since both have otherwise equal claims.

We are left with possibilities a, b and c. Although c (Hartert's) is logically correct, its re-adoption could lead to confusion and further

APPENDIX

Morphometrics of *Oenanthe leucopyga*. Populations numbered as in Fig. 1. Data are in the form: $\bar{x}$ ±1 SE (n) range.

Population	Wing	Tail	Bill	Tarsus
Males				
1	104.6±0.9 (10) 99–108	69.6±0.5 (10) 67–72	20.6±0.4 (7) 19–21	26.2±0.3 (10) 25–28
2	104.7±0.6 (9) 102–107	69.5±0.5 (8) 67–71	21.1±0.4 (9) 19–22	26.7±0.4 (9) 24–28
3	107.8±0.4 (11) 106–110	70.3±0.6 (11) 67–73	21.6±0.3 (10) 20–24	25.9±0.3 (11) 24–27
4	108.8±1.2 (5) 106–112	71.4±1.3 (5) 68–75	22.4±0.4 (5) 21–23	25.5±0.9 (4) 23–27
5	109.0±0.9 (11) 105–115	72.6±0.7 (12) 68–76	22.8±0.2 (12) 22–24	25.6±0.3 (11) 24–27
6	106.1±0.6 (19) 103–112	68.8±0.7 (19) 64–76	22.2±0.2 (18) 20–24	25.4±0.3 (18) 23–28
7	103.0±0.8 (5) 101–106	70.2±1.1 (5) 66–72	22.7±0.5 (4) 22–24	24.8±0.7 (5) 23–27
8	104.2±0.8 (10) 100–107	68.7±0.4 (10) 67–71	20.2±0.3 (9) 19–21	25.9±0.3 (10) 24–27
9	101.7±1.0 (6) 97–104	68.2±0.7 (6) 65–70	20.4±0.4 (5) 19–21	25.7±0.4 (6) 24–27
Females				
1	98.9±1.0 (8) 96–103	65.4±1.1 (8) 62–70	20.5±0.4 (8) 19–23	25.4±0.3 (8) 24–26
2	94 (1)	(0)	21 (1)	24 (1)
3	102.6±1.0 (12) 100–108	65.0±0.8 (11) 62–69	21.7±0.3 (10) 20–23	25.3±0.2 (11) 24–26
4	101 (1)	65 (1)	20 (1)	27 (1)
5	103.2±0.6 (9) 101–106	66.9±0.6 (10) 65–70	21.4±0.2 (10) 20–22	24.6±0.2 (10) 24–26
6	98.9±0.5 (15) 95–103	65.3±0.7 (15) 62–71	21.6±0.2 (15) 21–23	24.6±0.3 (14) 23–27
7	103.0±2.0 (2) 101, 105	66.5±1.5 (2) 65, 68	22.0 (2) 22, 22	24.5±0.5 (2) 24, 25
8	98.1±0.9 (9) 92–101	65.4±0.7 (9) 62–69	19.9±0.2 (9) 19–21	25.0±0.2 (9) 24–26
9	97.3±0.7 (3) 96, 98, 98	64.3±1.2 (3) 62, 65, 66	19.7±0.3 (3) 19, 20, 20	25.3±0.3 (3) 25, 25, 26

pointless nomenclatural discussion. My inclination with indistinct subspecies and clinal variation is to favour the suppression of all names for subspecies which are simply ends of a cline, while recognizing that variation exists, i.e. scheme b. However, the existing names will undoubtedly continue to be used to describe the various morphs. Hence, as subspecific names have been published, both of which describe recognizable populations, and since the type of the species belongs to an intermediate population, it may be safest to continue to use all 3 names, restricting the nominate to populations 3, 6 and 7 as in scheme a, or only to 3 and 6.

The above examination of tail pattern and morphometrics reveals that the previously-described subspecies are rather poorly-differentiated, though recognizable. I hesitate to complicate the nomenclatural situation further by pointing out that population 7 seems one of the best-differentiated, as well as being geographically isolated and that it, if any, deserves glorification with its own name.

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Notes on the birds of Buton (Indonesia, southeast Sulawesi)

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The author stayed on the island of Buton (Butung) 19 July–4 August 1981 and made observations on its birds. The most recent publication on the birds of Buton and Muna at that time was by van Bemmel & Voous (1951), who give a survey of the records from the literature and from collections. For this work G. A. L. den Haan collected on Buton and Muna in September and October 1948. van Bemmel & Voous also give an account of the zoogeography and a short description of the vegetation and geology of